FURTHER CONSIDERATION OF THE SHELL OF CHELYS AND OF THE CONSTITUTION OF THE ARMOR OF TURTLES IN GENERAL

By Oliver P. Hay

Associate of the Carnegie Institution of Washington

1. SUPERFICIAL, OR EPITHECAL, BONES

In 1922 the writer contributed an article to the *Journal of Morphology* [1] entitled "On the Phylogeny of the Testudinata and the relationships of *Dermochelys*." In this paper he called attention to the occurrence of certain plates of bone on the carapace and plastron of specimens of the South American pleurodire tortoise *Chelys*, known as the matamata. Some of the specimens studied belong to the American Museum of Natural History, New York; others are preserved in the United States National Museum. In the case of some of the shells there are many small bones irregularly distributed over the upper and the lower surfaces. The origin and nature of these were not determined. Other and usually larger bones occurred at definite points and were interpreted as relics of a primitive superficial armor retained nearly complete by the great sea turtle known as the leatherback, or *Dermochelys*. These bones were shown to occupy positions which correspond to 5 of the 12 keels which exist on the shell of *Dermochelys*, 7 on the carapace, 5 on the plastron.

After the publication of that article another matamata reached the United States National Museum from the Zoological Park at Washington and, inasmuch as this specimen presents many such bones, it is here described and illustrated by reproduced photographs. (Pls. 1 and 2.) From the front of the carapace to its rear the length is 13.5 inches (338 mm.). As in other specimens, there are on the carapace three prominent keels, a median and two lateral. The median keel presents five bosses or tuberosities, one at the rear of each vertebral scute. The hinder two are high and pointed. In each lateral keel are four such tuberosities, one at the upper rear corner of each costal scute. The marginal bones (peripherals) have each a projec-

[1] Vol. 26, pp. 421–445, with 2 pls.

tion or tuberosity of greater or less prominence; and these are placed along the sharp border of the carapace, one at the rear of each marginal scute.

From the carapace and plastron of the matamata here studied the scutes have been removed, and this has brought into view the superficial (epithecal) bones mentioned above. The epithecal bones of the plastron (not figured) occupy about the same positions as shown on plate 2 of the paper in the *Journal of Morphology;* but are more strongly developed. The one on the right gular scute spreads backward on the humeral scute. No such bone occurs on the hinder outer corner of the humeral scute areas of either the new specimen or of the ones previously described. From the front of each pectoral scute to the rear of the plastron there is a nearly continuous series of thin overlying bones. In the United States National Museum is a mounted skeleton of *Chelys* (Cat. No. 29545) whose epiplastron has along its whole lower border a rough surface which once supported an epithecal bone, where widest about 10 mm.

On the carapace (pl. 1) a minute ossicle is seen on the rear of the nuchal scute. On the boss situated about three-fourths of an inch in front of the hinder border of the first vertebral scute a scale of bone is to be expected. It is not present exactly there, but just a little in front of this there appears once to have been a narrow scale about 11 mm. long. Close to the rear of the second vertebral scute is a very distinct irregular ossicle, 10 mm. long and nearly as wide. Surmounting the tuberosity of the third scute is a bone about 12 mm. square forming an inset in the fifth neural bone. A smaller ossicle caps the fourth tuberosity. On the crest of the sharp ridge traversing the fifth vertebral scute area are several pits from which ossicles seem to have been torn away with the horny scute.

On the lateral keel of the left side the first, second, and third tuberosities support each a distinct bone, but there is none on the fourth. The same statement may be made about the tuberosities of the right lateral keel, but an ossicle on the third was evidently carried away on the horny scute.

On the left border of the carapace no epithecal bone appears on any of the first three tuberosities, but on the second scute, at the middle of the border, is a scale 10 by 15 mm. which may be looked upon as having migrated from the tuberosity just behind it. On the fourth tuberosity is a pit showing that a bone was torn away with the scute. On the left fifth scute area is a nearly circular bone 10 mm. in diameter, capping the boss. No superficial bone is seen on the sixth marginal scute. On the rear of the seventh scute area is a deep pit where a bone 20 mm. long was lodged; in fact, a part of it remains. On the rear of the eighth scute area is a scar or rough surface from which a superficial bone has been removed. Immediately above this rough surface is a patch of superficial bone 10 mm. high and 5 mm. wide, and this is to be regarded as a part of the bone which occupied the scar. On the rear of the ninth scute area is a pitlike scar, 10 mm. long, which doubtless supported a nodule of bone. On the tenth, eleventh, and twelfth scute areas the apices of the toothlike projections of the marginal bones are rough and evidently were beset with minute ossicles.

On the right border of the carapace a rough sutural surface is seen on the fourth scute area, while on the front of the fifth area is an excavation which gives the impression that the bone of the fourth area was nearly 30 mm. long and overlapped on the fifth area. On the rear of the sixth area was a minute ossicle. A rough articular surface on the rear of the seventh scute area indicates the former presence of a bonelet 10 mm. long. A long splinter of bone, part of which remains, ran along the whole lower border of the eighth scute area, while on the rear of the ninth is a very distinct scale of bone 5 mm. in diameter. On the border of the tenth area is a rough articular surface, and a similar one is present on the eleventh. On the twelfth area, near the midline, is a scale of bone 22 mm. long, loose, and almost ready to drop out of its place.

2. RESULT SECURED BY DR. H. VÖLKER

In my paper of 1922 I endeavored to meet some of the arguments advanced by Doctor Versluys against my views regarding the position of *Dermochelys*. In so limiting myself I did not do justice to Dr. Heinrich Völker, who, under the direction of Doctor Versluys, investigated in a thorough manner the skeleton of the trunk, of the limbs, and of the skin. His results were published in 1913.[2] On his page 516, Doctor Völker accepts the view that on the dorsal and ventral sides of *Dermochelys* we must distinguish two layers of dermal bones, a superficial (epithecal) and a more deeply placed layer (thecal). To the epithecal, he concluded, belong the dorsal shield, or armor, and the ossifications of the five longitudinal keels of the ventral side. To the thecal layer belong the nuchal bone, perhaps vestiges of costal plates retained on the ribs, and the bones of the plastron. The earliest recognition of these two wholly distinct layers of bone, Völker says, is to be credited to the present writer. On his page 526 Völker wrote "Mit Hay und im Gegensatz zu Dollo (1901) nehme ich für die gemeinsamen Vorfahren von Atheken und Thecophoren den Besitz eines Doppelpanzers an."

On only one important matter, as regards the structure of the shell of the thecophorous turtles, does Doctor Völker differ from

[2] Spengel's Zool. Jahrbücher, Abt. Anat. Ontol., vol. 33, pp. 431–552, pls. 30–33 and 3 text-figs.

me. He insists that the peripheral bones are equivalent to the bones of the marginal keels of *Dermochelys* and belong, therefore, to the epithecal layer, while I have regarded them as belonging to the deeper layer. In my original paper [3] I could rely only on the relation of the marginal scutes to the underlying bones of tortoises in general and on certain bosses on the peripherals of *Toxochelys* to sustain my view. Now, however, that these epithecal bones have been discovered on the median and lateral keels of *Chelys* and on its peripherals, I do not see how Doctor Völker or anybody else can refuse to accept my identifications. It is evident that the thecophorous peripherals were not derived from the athecate marginals. With the acceptance of this view Doctor Völker would be relieved of his difficulty (his page 525) in explaining how it happens that the horny scutes do not coincide with the peripherals.

On his page 530, Völker concedes that the suprapygal bones belong to the thecal skeleton, in view of my discovery that these in *Toxochelys* were overlain by epithecal elements, but he insists that the pygal bone is an epithecal bone. As he says, "Neither *Dermochelys*, nor *Archelon*, nor *Protostega* offers a solution of the question." To this may be said that *Chelys* does offer the solution. This bone is covered by the rear ends of the twelfth marginal scutes. As told above, on the twelfth scute area of the right side is a large loose bone (pl. 2, fig. 1) 20 mm. long. A few millimeters above it is another small scale of bone. Near the upper left border of the pygal (same figure) is tightly embedded an epithecal scale.

In evaluating the affinity of *Dermochelys* with the Cheloniidae Doctor Völker places the supposed epithecal marginal bones in the balance in favor of a close relationship. If we accept his view the elements of the shells of the Thecophora and of the Athecae may be thus expressed (his page 530):

	Thecophora		Athecae
Thecal elements	Nuchal. Neurals. Costal plates. Plastral bones.	Thecal elements	Nuchal. Possible shreds of costal plates on the ribs. Plastrals.
Epithecal elements	Marginal bones. Pygal. Vestigial shreds on the keels of rare species.	Epithecal elements	Dermal armor, upper and lower. Marginal bones.

If now the marginal elements and the pygal of the Thecophora belong to the thecal layer, as shown above, the statement will stand thus:

[3] Amer. Naturalist, vol. 32, 1898, pp. 929–948.

Thecophora		Athecae	
Thecal elements	Nuchal. Neural plates. Costal plates. Marginal bones Suprapygals. Pygal. Plastrals.	Thecal elements	Nuchal. Vestigial shreds on costal plates. Plastrals, greatly reduced.
Epithecal elements	Vestigial ossicles on the keels of a few species.	Epithecal elements	Upper and lower dermal armor, including the ossicles of the marginal keels.

When we consider the fact that the thecal elements of the Athecae are nearly as much reduced as the epithecal of the Thecophora it must be admitted, I believe, that the two groups are pretty widely separated.

3. ORIGIN OF THE PERIPHERAL BONES

In my paper of 1922, on page 426, I suggested that the thecal peripherals of the Thecophora may have arisen from a series of bones at the outer ends of gastralia. At present I am inclined to look on them as a row of bones developed one at the distal end of each of the costal plates. The costal plates and these hypothetical peripherals would have the relative positions of the large dorsal and the small lateral plates seen in the figures of *Aëtosaurus*. The third peripheral may be regarded as belonging to the first costal plate, that overlying the second rib. The first rib is greatly reduced and no costal plate is developed in connection with it. Nevertheless, its distal plate may have bene retained as the second peripheral. Usually no neural plate is developed which corresponds to the first dorsal vertebra, but in some species of Trionychidae, as *Aspideretes gangeticus* (Cuvier), there is present a plate of bone, the praeneural which seems to belong with that vertebra. At present it appears to me that the nuchal bone may be a plate homologous with the neural plates and to have been in relation with the neural spine of the last less cervical. In some ancestor a cervical rib may have been overlain by a plate of bone, long ago absorbed; but an accessory plate at its distal end may have been preserved and have become the first thecal peripheral.

4. RELATION OF THE NUCHAL TO THE EIGHTH CERVICAL VERTEBRA

Much importance is attached to the connection between the nuchal plate and the neural spine of the eighth cervical in the leatherback and the other sea turtles. If the writer's suggestion is correct that the nuchal bone is a homologue of the dorsal neural plates the connection mentioned above is a primitive one. In the great majority of tortoises this connection was lost, in order to facilitate the withdrawal of the head and neck into the shell or alongside of it. In the seafaring turtles the articulation may have been retained as a point of suspension for the head and neck.

5. SUBORDERS OF THE TESTUDINATA.

Tortoises must have existed already at some time during the Permian, for in the Triassic they appear with all their essential characters. In the Permian all the species may have belonged to one family, but differentiations had begun. There were yet probably none which could withdraw the head within the shell or hide it under the edge of the carapace. No definite cervical vertebrae yet existed, but in place of each a congeries of cartilaginous or bony basalia. Nevertheless there were tendencies which later revealed themselves in the normally bent neck of the Cryptodira and that peculiar to the Pleurodira.

Every chelonian is related to every other one of the order, but to some more closely than to others. I grant that *Dermochelys* is connected with the Cheloniidae more closely than with any other family of the order. In the undifferentiated condition of Permian days the ancestors of the Athecae and of the Cheloniidae may have been intimately related, but when the primal athecate broke away from the association, chose a life on the high seas, began to throw off the armor preferred by the others of his tribe and clothed himself with another, he won the right for his descendants to be regarded as a separate branch of the testudinate host.

Doctor Völker recognized the considerable differences existing between the Athecae and the other sea turtles, but he insisted that to regard the two as belonging to distinct suborders gave a very false conception of their kinship. He concluded (his page 512) that the relationship was best expressed by making *Dermochelys* and the other sea turtles a superfamily of the Cryptodira. If, however, this is done the other Cryptodira must constitute another superfamily and these two will form the suborder of Cryptodira. Then the Pleurodira and Trionychoidea must in their turn be given the rank of suborders. The writer believes that the Emydidae, Trionychidae, and the Chelyidae do not differ sufficiently from one another to be representations of as many suborders. Furthermore, Doctor Völker's scheme by no means brings out the great differences which have been demonstrated and which he concedes as existing between *Dermochelys* and the Cheloniidae. The writer maintains that the relationships between the groups of the Testudinata are best expressed by setting off the Athecae as a suborder opposed to the Thecophora.

6. RELATION OF THE COSTAL PLATES TO THE RIBS

In the carapace of the thecophorous chelonians the broad costal plates are intimately fused with the underlying ribs. If my explanation of the construction of the carapace is correct, those costal plates at some time in the history of these animals were free from the ribs; also it is probable, or at least possible, that in the embryologic development of some existing species the costal plates will be found to arise by distinct centers of ossification and only later to fuse with the ribs. Eminent naturalists have argued on this side of the question; others on that; a few, possibly, on both sides. Apparently Goette was the first to make a thorough investigation of the embryonic development, and he appeared to prove that the costal plate had in it no element of dermal bone. Nevertheless, Völker found himself driven to conclude that Goette was in error. A Japanese naturalist, Ogushi,[4] working on a species of soft-shelled tortoise (*Trionyx*), found that Goette's explanation compelled the conclusion that the scapula, which in other vertebrates overlies the ribs, has been brought to articulate by its distal end with the underside of the second rib. For this and other reasons Ogushi rejected Goette's hypothesis. Joan B. Proctor,[5] in studying the early stages of the remarkable land tortoise, *Testudo loveridgii*, found important evidence that the costal plates originated independently of the ribs.

7. RELATION OF THE HORNY SCUTES TO THE UNDERLYING BONES

Völker (his page 523) discusses the relations of the horny scutes to the underlying bones. He agrees with me that primitively the scutes coincide with the epithecal ossicles and that now in the thecophorous turtles the coincidence no longer exists. Each horny scute may cover parts of from two to as many as 10 bones. In my paper of 1898 I connected this expansion of the scutes with that of the epithecal bones, expressing the view that these bones may once have occupied most of the space now covered by the horny scutes of the living turtles. It is, however, not necessary to suppose that they were so large; although, to judge from *Chelys*, some of them must have had a respectable size. It can hardly be doubted that the scutes of the Pleurodira and the Cryptodira had their origin on the dominant epithecal bones of the keels of their early ancestors. In the primitive Thecophora the bones of the deeper layer were gaining the ascendency at the expense of the superficial ones. Although the expansion of the epithecal ossicle was checked, the overlying scute continued to grow. We must suppose further that the space between the keels was in some cases occupied by small plates of bone, as now

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[4] Morphol. Jahrb., vol. 43, 1911, pp. 13–15.
[5] Proc. Zool. Soc. Lond., 1922, pp. 483–526, pls. 1–3, 21 text-figs.

in *Dermochelys*, and that each of these was capped by a horny scute. Expansion of the large scutes was probably accomplished, not by suppression of the small scutes, but by fusion with them. As the small scutes were incorporated in the various dominating ones, the underlying ossicles may sometimes have long persisted and have produced the appearances reported in my paper of 1922.

Attention may be called to the point of origin of the scutes of *Chelys* and the direction of their expansion; also to the fact that the scutes of our land and swamp tortoises develop in the same manner. The vertebral scutes of *Chelydra* and of *Clemmys* (pl. 2, fig. 2) have the focus of their growth near their hinder border and they expand forward and laterally. The center of growth of the costal scutes is usually near the upper hinder border of the area and the expansion is upward, forward, and principally downward. The focus in each marginal scute is on the edge of the carapace, at the rear end of the scute; and the growth is directed forward and away from the border on both the upper and the lower side of the shell. This correspondence of the centers of origin and growth of the scutes of all the scute-bearing chelonians furnishes strong evidence that these centers correspond to the bony patches found on the tuberosities of *Chelys* and to bones in the keels of *Dermochelys*.

It is interesting to observe that in the case of all the scutes the growth is mostly forward, very little, or not at all, backward; and it is somewhat difficult to determine the reason therefor. At present it seems probable that it is connected with the growth of the front part of the shell to the end of furnishing a retreat for the head and forelegs. This has been accomplished principally by the forward expansion of the nuchal, the first costal plates, and the anterior 2 or 3 peripherals. As the nuchal borders moved forward and laterally the growth of the first vertebral scute was in the same directions and little energy was left backward growth. Naturally the second vertebral scute grew forward to fill the space left vacant; and so for the succeeding scutes. The same explanation appears to serve for the costal and the marginal scutes.

On the lower side of the shell the anterior plastral bones expanded forward and inward. The median, or interplastral, row of epithecal bones, with their scutes, were early suppressed, so that the definitive scutes were supplied from the bones of the lateral plastral keels. As a result we find that the horny scutes have their centers of growth on the outer and rear borders.

In most Thecophora there are left few or no indications of the inframarginal keels of *Dermochelys* except perhaps the scutes at the ends of the bridges. In species of *Baëna* there is on each bridge a row of large inframarginal scutes. Where such scutes are missing the space is filled by outward expansion of the humeral and abdominal scutes. In *Terrapene* the space is obsolete.

It seems worth while to try to account for the extension of the scutes beyond the bone on which they originate. Briefly expressed the explanation is that they were originally associated each with an epithecal bone which later ceased to support it, leaving it to wander until it reached the obstructing border of its neighbors. Sometimes parts of three or more bones are traversed to meet the boundary; sometimes only two. By the superior growth of epithecal bones along certain lines the keels of the early ancestors of turtles were produced. In the course of time some of the bones of the keels became enlarged at the expense of other bones and of the scutes overlying them. Along the middle of the back of *Toxochelys* we find enlarged epithecals reposing on the neurals. We may suppose that the most favorable position of an epithecal would be on or near a suture between two neurals, since blood vessels and nerves could more readily reach it. If now an epithecal of the size of those of *Toxochelys* were lodged across each neural suture the neural bone itself would tend to be suppressed; and among the early Thecophora the neurals themselves were gaining the upper hand. Hence about alternate epithecals were suppressed. Although the dominating epithecal was itself later dispensed with, the horny scute associated with it would expand forward to reach the scute situated the length of two neural plates in front. The same explanation will apply to the fore-and-aft width of the costal scutes, which may cover one costal bone, a part of the one behind, and a part of the one in front.

When we examine the marginal scutes we find each one covering a portion of one peripheral and a larger portion of the next peripheral in front. It seems to the writer that the explanation is as follows: The epithecals of this row were small and one for each peripheral did not menace the development of the latter. Hence its scute could spread only over a part of the next peripheral in front.

8. DR. G. K. NOBLE'S OBSERVATIONS ON CHELYS

In 1923 Dr. G. K. Noble reviewed my paper[6] of 1922 and gave an interesting account of his observations made on a young matamata of about three-eighths the size of the animal described in the present article. In his specimen he was able to find no traces of the epithecal bones. Considering this young animal in connection with the adult in which the bones were absent Noble concluded that my "hypothesis should not be accepted without additional materials." The present paper describes the additional materials desired.

[6] Amer. Naturalist, vol. 57, pp. 377–379.

It must be remembered that we are dealing with structures which, as the writer maintains, became useless thousands of generations ago and ceased to be reproduced by the great majority of turtles. It is not strange, therefore, that they appear in the matamata irregularly and in some cases not at all. Doctor Noble must recall what happens in the case of the canine teeth of mares and of the first premolars of horses in general, not to mention other similar examples.

Doctor Noble appears to suggest the attacks of parasites on these captive matamatas, but he does not pursue the subject. The life history of such a parasite would be interesting, if it exists. Doctor Noble, however, finally concludes that the ossicles in question seem to be bony deposits over injuries received either during captivity or rarely in nature. He ought to have told us whether he has observed similar bony deposits beneath the uninjured epidermal scutes of snapping turtles and terrapins kept in confinement.

9. PROCTOR'S RESULTS FROM THE STUDY OF TESTUDO

Mention has just been made of the work of Joan B. Proctor on the anatomy of *Testudo.* In her effort to determine whether the costal plates are simply expansions of the ribs or originate independently of them that author examined the recently hatched young. She found that the embryonic costal plate was in contact with the rib; also that the rib was undergoing degeneration at a time when the costal plate was growing vigorously. She concluded, therefore, that the plate was not derived from the rib. She was led to consider also the relation of the developing horny scutes to these costal plates and in doing so she hit upon a condition which, then unknown to her, had been described by Richard Owen. In the young tortoise the horny scutes are already present and relatively large. Inasmuch as the vertebral scutes alternate with the costal scutes, there is along each side of the dorsal region a zigzag series of points, from each of which radiate the edges of three scutes. The author cited found that a costal plate developed immediately under each of these triradiate structures and that the forms of these plates in their early stages of development were in strict correlation with the sutures between the superincumbent epidermal shields.

Now, with few exceptions, and these probably of secondary origin, the plates and scales of dermal bone in reptiles underlie and support the horny scutes, and the two structures agree more or less exactly in form and size. If the explanation proposed by Proctor is correct the costal plates take their origin at the intersections of the borders of three scutes and these scutes determine the early forms of the plates. The present writer believes that these conclusions are erroneous. The presence of the bones beneath the borders of the scutes is a coincidence and these are not the cause of the ossification or of the forms of those plates. In the genus *Testudo* alternate costal plates are proximally broad, so as to articulate with three neurals; intervening ones are narrow. In the embryo figured the costals were preparing to assume those alternating forms. It will hardly be contended that the shapes finally taken by the costal plates, interlocking as they do, are determined by the horny shields. Furthermore, the proximal end of each embryonic plate is pretty certainly at the point where it quits the rib and reaches out to meet the neural plate. If the growth of the costal is determined by the epidermal shield the point where the rib becomes free ought to be just below the outer extremity of the vertebral scute. A study of the shells of a few species of tortoises will show no such relation. The vertebral shields may be very broad while the rib-heads are short.

It is the contention of the present writer that the horny shields of tortoises had primarily no relation to the costal plates, but to more superficial bones, the epithecals. As a result of the suppression of the epithecals the horny shields were brought into contact with the more deeply lodged thecal bones. In *Chelys* the epithecals are reproduced in many individuals and from these the horny scutes spread out over the thecal bones. The only effect the scutes appear to have on the thecals is to impress on their surface the radiating and concentric lines of growth. The shields do not grow at their edges merely, but a new layer of horn is laid down on its whole lower face, and these layers may often be separated from one another.

EXPLANATION OF PLATES

Plate 1

Chelys fimbriata

View of carapace from above. × 0.44

c. s. 1—c. s. 4. Costal scutes.
m. s. 1—m. s. 12. Marginal scutes.
n. s. Nuchal scute.
v. s. 1—v. s. 5. Vertebral scutes.

Plate 2

Fig. 1. *Chelys fimbriata*

View of rear of carapace from behind. × 1

To show specially the large epithecal bone on the twelfth marginal scute.
m. s. 11, m. s. 12. Eleventh and twelfth marginal scutes.
v. s. 5. Fifth vertebral scute.

Fig. 2. *Clemmys insculpta*

View of carapace from above. × 1

Shows the vertebral, costal, and marginal scutes, their areoles, the outcropping edges of the successive horny layers, and the direction of expansion.

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